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Long-term decline of a winter-resident bird community in Puerto Rico

John Faaborg · Wayne J. Arendt · Judith D. Toms · Katie M. Dugger · W. Andrew Cox · Miguel Canals Mora

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Abstract Despite concern expressed two decades ago, there has been little recent discussion about continuing declines of migrant bird populations. Monitoring efforts have been focused almost exclusively on the breeding grounds. We describe the long-term decline of a winter-resident bird population in Guánica Commonwealth Forest, Puerto Rico, one of the last remaining tracts of high-quality tropical dry forests in the Caribbean. The winter bird community has exhibited dramatic declines, with constant-effort mist netting now capturing about one-third as many birds as it did 20 years ago. Population estimates for the three most common species have declined dramatically, even though

J. Faaborg (✉) · J. D. Toms
Division of Biological Sciences, University of Missouri, Columbia, MO 65211-7400, USA
e-mail: faaborgj@missouri.edu

W. J. Arendt
International Institute of Tropical Forestry, US Forest Service, Sabana Field Research Station, HC 2 Box 6205, Luquillo, PR 00773, USA

Present Address:
J. D. Toms
Eco-Logic Consulting, 3014 Craigowan Road, Victoria, BC V9B 1M8, Canada

K. M. Dugger
Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331-3803, USA

Present Address:
K. M. Dugger
U.S. Geological Survey, Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331-3803, USA

W. A. Cox
Department of Fisheries and Wildlife Sciences, University of Missouri, 302 ABNR, Columbia, MO 65211, USA

M. Canals Mora
DRNA-Bosque de Guánica, PO Box 1185, Guánica, PR 00653-1185, USA

survival rates have remained constant, and other species are now virtually absent from a site where they once were fairly common. Although explanations for these declines are speculative, particularly because they involve multiple species, we argue that the strength and duration of these declines in well-preserved dry forest within a biosphere reserve should stimulate renewed discussion of migrant population trends and comparison with other recent monitoring activities.

Keywords American Redstart · Black-and-white Warbler · Ovenbird · Partners in Flight · Songbird population declines

Abbreviations

AIC_c Akaike's information criteria, corrected for small sample size
WNV West Nile Virus

Introduction

Many species of Neotropical migrant birds have experienced significant population declines over the past 40+ years (Robbins et al. 1989; Sauer and Link 2011), but identifying the causes of the declines is particularly challenging because complex life-cycles of migrants can involve multiple habitat types across vast spatial scales and migratory connectivity is not well understood for most species (Sherry and Holmes 1995). Much of the work to date has focused on factors occurring on the breeding grounds, and biologists have made tremendous advances that have helped inform conservation guidelines and management strategies (Faaborg et al. 2010a). Nevertheless, the efforts to understand population processes on the breeding grounds have not been matched elsewhere, with comparatively little work being done on habitat used during migration or on the wintering grounds. As such, basic information such as population densities or temporal trends in abundance on the wintering grounds is almost entirely lacking for most migrant birds (but see Johnson et al. 2006).

There is inherent value in monitoring changes in the abundance and diversity of wildlife (Danielsen et al. 2005), but the need to monitor migratory songbirds on their wintering grounds is particularly acute because densities are believed to be much higher there, to the point that Terborgh (1980) argued that loss of one hectare of wintering habitat could result in an equivalent loss of birds in as many as eight hectares of breeding ground habitat. High concentrations of birds combined with the fact that population trends are easier to detect when initial abundances are higher (Taylor and Gerrodette 1993) make the wintering grounds ideal for monitoring studies. Results from 18 years of monitoring in Puerto Rico showed declines on a single netline during 1973–1988 (Faaborg and Arendt 1989). These declines were noted by others as evidence of migrant bird declines on the wintering grounds (Terborgh 1989) and were part of the evidence supporting the development of the Neotropical Migrant Bird Conservation Program (now known as Partners in Flight). However, Faaborg and Arendt (1992) suggested the declines in the 1980s reflected breeding ground limitations, rather than problems within the tropics, in part because the winter resident numbers recovered during 1989–1992.

Here, we present additional results from an unprecedented 40-year monitoring project in Guánica Commonwealth Forest, a United Nations Biosphere Reserve in southwest Puerto Rico and one of the last remaining tracts of high-quality tropical dry forest in the Caribbean. Our goal was to describe declining trends in the diversity and abundance of migratory forest-breeding songbirds wintering in habitat that historically supported the highest densities of forest birds on Puerto Rico (Kepler and Kepler 1970).

Methods

We monitored winter resident bird populations each January since 1973 (except 1977 and 1979) in the Guánica Forest of southwest Puerto Rico, a 4,000 ha biosphere reserve known for the quality of its subtropical deciduous forest (Ewell and Whitmore 1973). Sampling methods are detailed in Faaborg et al. (2004). Briefly, we operated one 200 m netline annually during 1973–1988 (except 1977 and 1979) but we have had a much larger sampling effort for the past 24 years. We added six new netlines in 1989, a seventh in 1990, and an eighth in 1991. We have run the same nine lines in January since 1991, totaling 1,800 m of mist-nets. Movement of individuals between netlines is rare (J. Faaborg, unpublished data), indicating that they can be considered independent samples. We chose netline locations that included most of the microhabitats within the reserve, with most habitat variation related to slope or disturbance history. Assuming these lines catch birds moving within 50 m of the netline (which is a reasonable estimate given our knowledge of movements and territory size of resident and winter resident birds; Toms 2011), each netline covers 2.78 ha (7 acres), and we sample 25 ha (62 acres) in total. For logistical reasons the lines were centrally located within the reserve.

We operated each netline for three consecutive days from dawn to dark. We marked all captured birds with uniquely numbered aluminum bands provided by the USGS bird banding lab and released them at the point of capture. Permission to handle these birds was granted by the University of Missouri Animal Care Committee, the USGS bird banding lab, and the Puerto Rican Department of Natural Resources.

All statistical analyses were conducted using only the intensive netting data (1989–2012). We used capture/recapture models to estimate survival rates and capture probabilities with R-Mark (ver. 2.0.9; Laake 2011). A separate model was constructed for each of the three most frequently caught species, American Redstart (*Setophaga ruticilla*), Black-and-white Warbler (*Mniotilta varia*), and Ovenbird (*Seiurus aurocapilla*). All other winter residents were grouped together for analysis. We used Program RELEASE (Burnham et al. 1987) to test for transient individuals and trap-shyness, but there was no evidence for these effects. We tested constant and non-constant time-varying survival submodels. Capture submodels tested were constant, linear trend in capture rates, non-linear time-varying capture rates, capture rate dependent on rainfall in the first six months of the year (which is highly correlated with breeding season rainfall), and capture rate dependent on rainfall in the second six months of the year (which is highly correlated with non-breeding season rainfall). In addition, models for the grouped winter residents also included a capture submodel allowing capture rates to vary across species. Full survival models fit included all combinations of survival and capture submodels. However, constant survival models were strongly supported by the data in all cases. Raw capture totals were then inflated by the model-averaged capture probabilities to estimate total population size, including adjustments to account for the reduced number of netlines in 1989 and 1990. Variances for these estimates were calculated using the delta method (Dugger et al. 2004) and used to derive 95 % confidence intervals. Total winter resident population size was then determined by summing the individual population estimates for American Redstart, Black-and-white Warbler, Ovenbird and other winter residents, with variance estimates adjusted assuming errors were not correlated across these species groups. Finally, we assessed whether substantial declines in individual species or total winter residents occurred by comparing a set of constant, linear decline, and piecewise regression (Toms and Lesperance 2003) models (with a tanh transition), using Akaike's information criterion corrected for small sample size (AIC_c) within a model-selection framework (Burnham and Anderson 1998). We calculated the difference between the top model and other candidate models (ΔAIC_c) and used the ΔAIC_c values to calculate weights (w_i) and evaluate the relative support of each model in the candidate set.

We used the capture data to model true species richness in Program SPADE (Chao and Shen 2010) using the incidence-based coverage estimator (ICE; Colwell and Coddington 1994; Lee and Chao 1994; Chao and Shen 2010), which allows for heterogeneity in species detection probability and performs well when several species have low detection probabilities. We treated netlines as replicate samples. We assessed whether species richness declined significantly by comparing a set of constant, linear decline, and piecewise regression models as above.

Results

Our long-term study using constant-effort mist netting shows a collapse of both the abundance and diversity of wintering birds over the past decade. Estimated abundance of all winter residents combined fluctuated around a common mean from 1990 to 2001, but declined dramatically beginning in 2002 (Fig. 1). A comparison between constant, linear trend, and piecewise regression models indicated strong support for a negative linear decline for winter residents (Table 1) with local extirpation of the winter resident community predicted in 2030. Species richness estimates also declined from 1989 to 2012 (Table 1), though the confidence interval just included zero.

The three most common winter resident species, which historically comprised 75 % of winter resident captures, all show population declines during this period (Table 1; Fig. 2): Black-and-white Warblers declined from over 250 birds in 1991 to fewer than 50 birds for four of the past five years; Ovenbirds also declined, with 8 of the 10 lowest estimates in the last nine years. American Redstarts averaged 155 birds during 1990–2004, but only 87 birds since 2005, though model-selection uncertainty suggests this trend is less pronounced than for Ovenbirds or Black-and-white Warblers (Table 1). Despite the significant declines in these populations, survival rates were estimated to remain constant over this time for all three species (Black-and-white Warbler 0.523 95 % CI: 0.512–0.534, Ovenbird 0.492 95 % CI: 0.477–0.506, and American Redstart 0.607 95 % CI: 0.563–0.651).

In addition, other migrant species regularly captured during the early years of this study have declined or disappeared entirely from the Guánica Forest (Table 2). Species caught virtually every year during the 1990s but of much lower occurrence recently include the Northern Parula (*Setophaga americana*), Prairie Warbler (*Setophaga discolor*), Worm-eating Warbler (*Helmitheros vermivorum*), and Hooded Warbler (*Setophaga citrina*). These species were captured in nearly all years early in the study, with at least 10 captures per species in some years (Table 2), but they have been sporadic recently, with some years showing no captures. For example, Worm-eating Warblers were captured regularly from 1989 to 1997, and ten of the first 28 birds were recaptured multiple times over spans ranging from 4 to 10 years. Since 1998, we have had only one recapture of a Worm-eating Warbler, and in three of the past 6 years we have had no captures of this species. Similar patterns among additional less common species contribute to the overall decline in winter resident abundance and diversity.

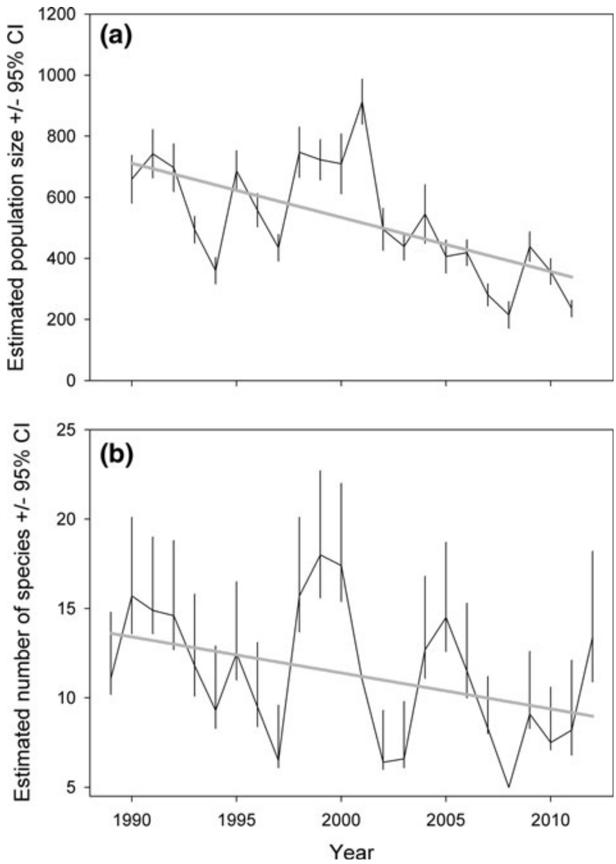

Fig. 1 Annual variation in estimates of total winter resident birds from 1990–2011 (**a**) and estimated species richness from 1989–2012 (**b**) for winter residents with fitted negative trends from capture/recapture data gathered from nine netlines in the Guánica Forest, Puerto Rico. *Error bars* are 95 % confidence intervals

Discussion

Understanding population regulation in long-distant migrants is notoriously difficult (Faaborg et al. 2010b). Apparent survival rates of wintering migrants have remained constant over time at this study site (Dugger et al. 2004, this study), which suggests that population declines are driven by declining recruitment of birds into the forest. However, it is not clear why recruitment may have declined. Historically, winter-resident captures declined following drought conditions on their breeding grounds, but in all prior instances depleted populations recovered with the return of breeding season rainfall (Faaborg and Arendt 1992; see increases in 1995 and 1998–2001 in Fig. 1). The onset of this decline in winter residents corresponds to the appearance of West Nile Virus (WNV) across the breeding range of these species, but warblers (>98 % of our captures) are not thought to be susceptible to WNV (LaDeau et al. 2007). Capture rates from a netline operated at this site since 1973 suggest that American Redstart and Ovenbird declines began 40 years ago (Fig. 3), as has been shown also for some old world long-distance migrants (Sanderson

Table 1 Model-selection results describing population trends of all winter residents, trends for the three most common winter resident species, and changes in species richness in Guánica Forest, Puerto Rico, 1989–2012

	K^a	AIC_c^b	ΔAIC_c^c	w^d	Trend ± 95 % CI
Population trends					
All winter residents					
Linear	3	288.77	0.00	0.83	−17.72 ± 10.02
Piecewise	6	292.18	3.41	0.15	
Constant	2	296.42	7.65	0.02	
American Redstart					
Linear	3	244.05	0.00	0.55	−3.29 ± 3.63
Constant	2	244.58	0.53	0.42	
Piecewise	6	250.28	6.23	0.02	
Black-and-white Warbler					
Linear	3	221.59	0.00	0.99	−8.94 ± 2.18
Piecewise	6	231.06	9.47	0.01	
Constant	2	250.64	29.05	0.00	
Ovenbird					
Linear	3	230.85	0.00	0.91	−3.92 ± 2.68
Constant	2	235.70	4.85	0.08	
Piecewise	6	240.22	9.37	0.01	
Species richness					
Linear	3	133.44	0.00	0.64	−0.20 ± 0.20
Constant	2	134.63	1.19	0.35	
Piecewise	6	143.12	9.68	0.01	

Population trend values indicate the annual change in the number of individuals captured. The species richness trend value indicates the annual change in the number of species captured

[a] Number of parameters in the model

[b] Akaike's information criteria, corrected for small sample size

[c] Difference between the AIC_c score of the current and top-ranked model

[d] Weight of evidence supporting the model

et al. 2006). Hurricane Georges caused extensive short-term habitat damage in 1998, but did not affect survival rates of either resident or winter resident populations (Dugger et al. 2004), and winter resident captures peaked in 2001. Long-term rainfall variation associated with global warming may be affecting overall habitat quality (Singh 1997), which might lead winter residents to go elsewhere after they appear in the fall, but those birds that choose to spend the winter at Guánica survive and return at the same rates they always have (Dugger et al. 2004).

Habitat within Guánica Forest has not changed in any obvious fashion from when it supported impressive numbers of winter resident warblers. The extensive damage to the forest canopy caused by Hurricane Georges in 1998 occurred well before the decline began; in fact, our highest ever capture rates and population estimates occurred after the hurricane. It has been suggested that wintering birds may have moved to other forests on Puerto Rico, as the amount of forest cover on the island has been increasing. However, these forests are distinctive because they are primarily second-growth vegetation, occur at

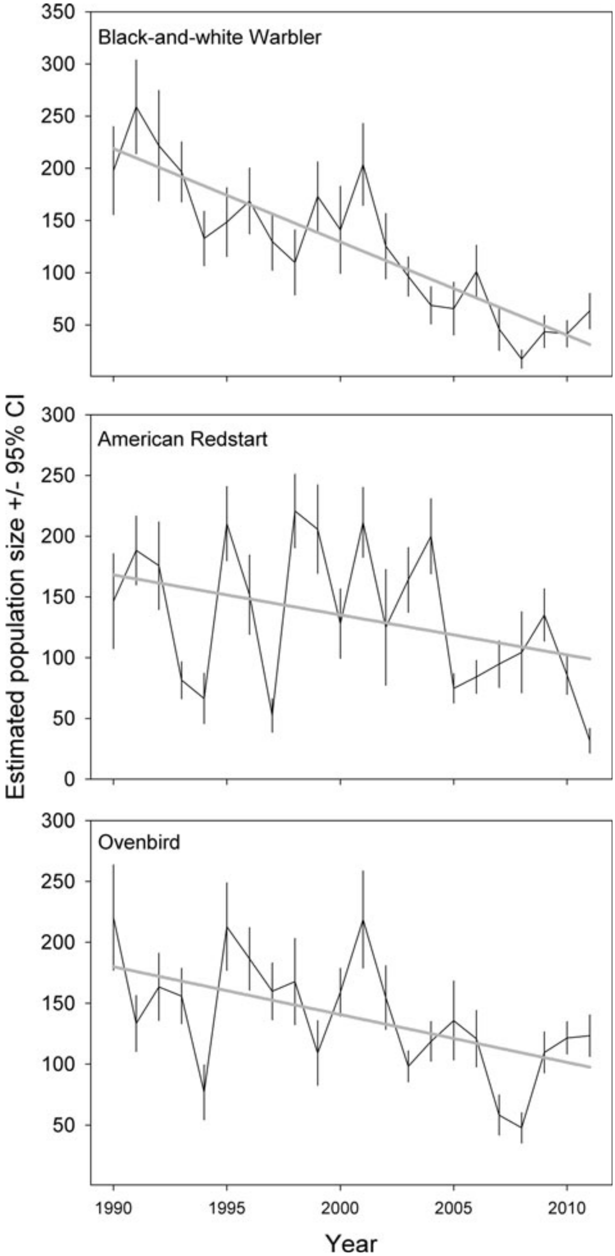

Fig. 2 Declining population estimates for the three most common species captured in our study, computed using MARK. *Error bars* are 95 % confidence intervals

higher elevations, and tend to support low abundances of all birds (Kepler and Kepler 1970). In contrast, dry forests such as Guánica have historically supported higher bird densities and species diversity than wetter habitats, both on the island (Kepler and Kepler 1970, Tossas, Toms and Arendt, unpublished) and in the surrounding region (Lack 1976;

Table 2 Number of winter residents captured annually from 1973–2012

Species	73–88	89	90	91	92	93	94	95	96	97	98	99	00	01	02	03	04	05	06	07	08	09	10	11	12
Merlin (*Falco columbarius*)		1	1							1	1		1		1										1
Bicknell's Thrush (*Catharus bicknelli*)	1																	1							
Ovenbird (*Seiurus aurocapilla*)	23	26	51	29	35	34	18	44	38	33	34	22	31	41	30	16	20	24	23	11	8	18	20	20	13
Worm-eating Warbler (*Helmitheros vermivorum*)		4	2	6	5	2	3	8	7	10	3	7	5	5	1	3		5	6	2		2			1
Northern Waterthrush (*Parkesia noveboracensis*)	1		2	4	1				2			1													
Blue-winged Warbler (*Vermivora cyanoptera*)												1													
Black-and-white Warbler (*Mniotilta varia*)	66	35	52	60	67	38	38	50	56	34	41	43	44	45	26	26	15	16	26	12	5	14	12	12	14
Prothonotary Warbler (*Protonotaria citrea*)	5	2		1	1							1	3	6							3				
Swainson's Warbler (*Limnothlypis swainsonii*)			1		1	1								2			1		1	1					
Kentucky Warbler (*Geothlypis formosa*)												1						1							
Hooded Warbler (*Setophaga citrina*)	5	5	10	8	4	1	2	3	2		2	2	2	5			2	3		1		13	3	2	
American Redstart (*Setophaga ruticilla*)	71	13	21	19	30	11	9	29	21	7	34	18	16	24	16	23	14	9	7	10	10	11	8	2	5
Cape May Warbler (*Setophaga tigrina*)	17	2	1	9				3			1		1				3	2							

Table 2 continued

Species	73–88	89	90	91	92	93	94	95	96	97	98	99	00	01	02	03	04	05	06	07	08	09	10	11	12
Northern Parula (*Setophaga americana*)	31	4	3	7	8	7	4	7	1	2	22	15	17	15	10	1	6	5	7	7	5	6	6	1	1
Magnolia Warbler (*Setophaga magnolia*)				1		1		1			1	2	2	2											
Black-throated Blue Warbler (*Setophaga caerulescens*)			2	2																					
Prairie Warbler (*Setophaga discolor*)	18	2		4	12	4	10	5	2	6	21	19	16	13	10	12	13	8	7	4	1	4	6	1	3
Baltimore Oriole (*Icterus galbula*)																			1						
Indigo Bunting (*Passerina cyanea*)				1	1					5	1		1				1								1
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)								2			2		12	12			4	1	1			1	3		
Total winter residents	237	94	139	151	165	99	85	152	129	98	163	132	151	170	94	81	79	75	80	48	32	69	58	38	39

Captures from the single netline run from 1973–1988 are summed across years. Seven netlines were run in 1989, eight in 1990, and nine since 1991

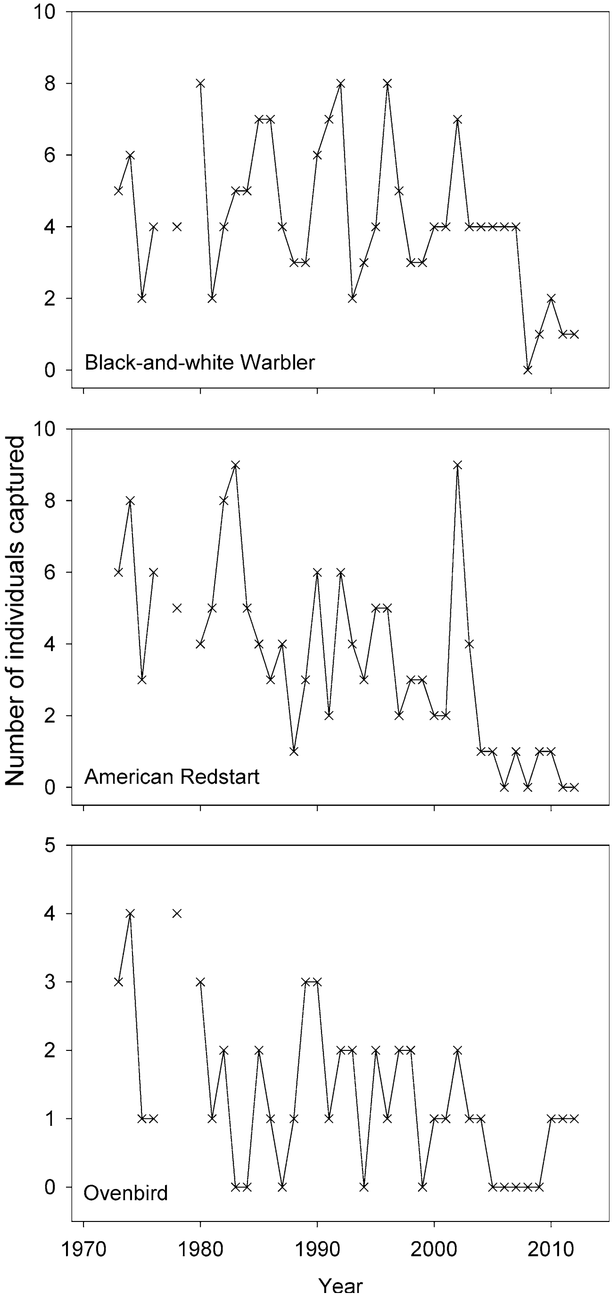

Fig. 3 Historical declines in capture rates for the American Redstart, Ovenbird and Black-and-white Warbler at a single netline operated annually from 1973 to 2012 except for 1977 and 1979. Note that the redstart shows a long-term pattern of decline, while the Black-and-white Warbler maintains fairly steady populations until the past decade

Terborgh et al. 1978; Terborgh and Faaborg 1980), and the amount of dry forest has not increased in recent decades. In addition, although this is a single study site, it involves nine 200 m netlines that include most of the microhabitats within the reserve and is thus remarkably extensive both in time (24 years for multiple netlines; 40 years for a single line) and space (at least 25 ha of coverage).

The Breeding Bird Survey shows stable or only gradually declining populations of our most common species in many regions within their breeding grounds (Sauer et al. 2011). On the other hand, Wilson et al. (2011) recently showed that American Redstart has been declining by 3.42 % annually in the Atlantic Northern Forest, which is where our wintering birds appear to breed (Dugger et al. 2004). Our data support the idea presented by Terborgh (1980) that migrant birds might have highly concentrated abundance patterns on the wintering grounds and show declines there first. Puerto Rico is on the edge of the principal Caribbean wintering range for many of these migratory species (Terborgh and Faaborg 1980; Arendt 1992; Wunderle and Waide 1993), and thus might be expected to show changes in population densities or wintering range before they are seen in core areas of the wintering range. Given that most migratory bird populations consist of regions of increase and decline (James et al. 1996), and that our knowledge of the linkage between wintering and breeding ranges is imprecise (Faaborg et al. 2010b), we feel that these data are noteworthy, no matter the broad-scale patterns on the breeding grounds.

We continue to explore plausible explanations for the observed decline of winter resident birds at our study site, but given the diversity of species involved and the complexities of each species' annual demography, perhaps that is an unrealistic goal. For example, our wintering populations of American Redstart are declining and their breeding populations have been shown to be declining as well (Dugger et al. 2004; Wilson et al. 2011). However, do we really understand why they are declining in either location? The fact that New England-breeding redstarts and southern-breeding Worm-eating Warblers are both declining on their shared wintering grounds suggests that the limitation occurs at Guánica, but the fact that survival rates for those birds that do return are constant argues for breeding season control of populations. For conservation purposes, can we afford to wait to publish evidence of community-wide declines until the decline of each species can be explained?

We know of no other published or unpublished data that exist from the wintering grounds of these warblers that could corroborate or dispute our findings; most current work on wintering birds started well after our recorded declines in populations in Puerto Rico. If the patterns shown by our study (Fig. 1) are in fact widespread, studies begun after the year 2002 might show patterns of population decline, but these would appear to be much less pronounced than those shown over the past 20–40 years in Puerto Rico. For example, if we run a regression for the total winter resident populations for the past seven winters, the decline shown is no longer statistically significant. Similarly, annual variability is likely to mask overall patterns in short-term studies.

Given the patterns shown by our data, we now join with those who earlier proclaimed that "the sky is falling" for Neotropical migratory birds, even though we lack a ready explanation for these declines. On the other hand, the discussions about the existence and possible causes for migrant bird declines that occurred 20 years ago helped stimulate the development of Partners in Flight. We invite other scientists to join us in understanding the patterns we have found, yet we caution that if the declines on the wintering grounds shown in our study are widespread, the baseline for current research is greatly changed and the populations they may study are already much reduced.

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